Frequenz nach Maßgabe der Verstärkungsgeschichte eine signifikante Veränderung erfahren. Über die Geschwindigkeit eines Lernfortschrittes entscheidet jedoch keineswegs die potentielle Lernfähigkeit in konstanter Weise, sondern vielmehr die Frage, ob der zu einem bestimmten Zeitpunkt eingesetzte Verstärker auf einen zu diesem Zeitpunkt maximalen Mangelzustand (Bedürfnis) trifft und diesen schrittweise und nach Maßgabe eines (verstärkten) emittierenden Operanten abzubauen vermag. Dabei wird die Wirksamkeit der Verstärkung in dem Maße reduziert, wie mittels des verstärkten Operanten über den Erhalt der Verstärkung der Mangelzustand beseitigt wird und damit die Reaktionsbereitschaft erlischt. Rein funktional kann diese Reaktionsbereitschaft als ,,Geschichte und Effekt einer Deprivation" (SKINNER 1973, 1974) definiert werden, z. B. als Dauer des Nahrungsentzuges. Die nicht unmittelbar aus äußeren Reizkonstellationen ableitbaren, ein (Lern-)Verhalten hinsichtlich Richtung und Intensität beeinflussenden Variablen können jedoch auch unter dem Begriff ,,Motivation" zusammengefaßt werden, wobei diese als Phase des Aktivitätskontinuums eines Organismus mit Einflüssen auf Intensitäts-, Richtungs- und Formveränderungen jeglicher Aktivität erkennbar wird (FOPPA 1965; SCHÄFER 1980, im Druck). Motivation als ,,Ergebnis einer Verstärkung und der Vorenthaltung des Verstärkers" (CORREL 1971) wird entsprechend dann als bestimmend für ein Verhalten erkennbar, wenn nur bestimmte, dem Erhalt einer Verstärkung zuzuordnende Handlungen allein und emittierend auftreten. Bei den vorliegenden Experimenten kann allein aus der Tatsache des häufigen (und freiwilligen) Aufsuchens der Apparaturen in diesem Sinne auf eine eindeutige Motivation geschlossen werden, die die beobachteten Lernfortschritte und die Brauchbarkeit des Zeitkriteriums erklären dürfte. Bestimmt hingegen der Experimentator zwanghaft den Beginn eines Versuches, so muß mit unterschiedlichen Reaktionsbereitschaften (Flucht, Erkunden, Schlafen, etc.) gerechnet werden, die die Einengung auf das zu verstärkende Verhalten zumindest erschweren. In diesem Sinne muß die Möglichkeit zur Arbeit mit freilebenden Individuen von *Erinaceus europaeus* als besonders günstige Voraussetzung der geschilderten Experimente hervorgehoben werden.

Zusammenfassung

Die Lernleistungen zweier freilebender Individuen von *Erinaceus europaeus* L. wurden in einem Manipulations-, einem Labyrinth- und einem Diskriminationstest untersucht. Die Tiere konnten nach Maßgabe ihrer eigenen Aktivität und Motivation die im Freien aufgestellten Apparaturen aufsuchen; als positive Verstärkungen wurde jeweils eine geringe Menge Milch eingesetzt.

Als Manipulationsaufgabe wurde eine mit einem Korken verschlossene Flasche geboten; die Zeitspanne zwischen der ersten Berührung der unter der Flasche aufgestellten Futterschale und dem Ergreifen und Herausziehen des Korkens konnte als Kriterium eines schnellen Übungsfortschritts herangezogen werden.

Zur Quantifizierung der Lernleistungen in einem einfachen T- Labyrinth konnte die benötigte Laufzeit verwendet werden; ein Umstellen der Milchschale in den anderen Schenkel bewirkte nach einer Trainingsphase zunächst Läufe zur nun leeren Seite, obwohl eine olfaktorische Orientierung zweifellos möglich gewesen wäre; ein Umlernen erfolgte in kurzer Zeit.

Zur Prüfung der optischen Diskriminationsfähigkeit wurden zwei mit Klappen verschlossene Wahlkammern benutzt; als positiver Hinweisreiz diente ein schwarzer Kreis auf der einen Klappe gegen ein schwarzes Quadrat auf der anderen. Nur ein Tier erreichte in 40 Tests einen signifikanten Anteil positiver Wahlen, die Aufenthaltshäufigkeit des zweiten Tieres erwies sich jedoch (trotz des nicht hinreichenden Anteils korrekter Wahlen) in Kontrollexperimenten als überwiegend dem positiven Muster zugeordnet.

Die auffallend raschen Lernfortschritte wurden in Bezug zum ,,Motivationsproblem" gefangener und freilebender Versuchstiere diskutiert.

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Thermoregulation, oxygen consumption, heart rate and evaporative water loss in the thick-tailed bushbaby (Galago crassicaudatus Geoffroy, 1812)

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Abstract

Studied were thermoregulation, oxygen consumption, evaporative water loss and heart rate in the thick-tailed bushbaby (*Galago crassicaudatus*). O_2-consumption was lowest at ambient temperatures (T_a) from $25-31\,°C$. Within this thermoneutral zone (TNZ) the basal metabolic rate (BMR) was only 71% of the value expected from body mass. At $T_a = 5\,°C$ O_2-consumption nearly doubled. The body temperature (T_b) exhibited a marked day-night-rhythm. The mean resting T_b was $36,6\,°C$; during activity the mean level rose to $37,7\,°C$. Low ambient temperatures did not affect the body temperature, whereas at $T_a = 38\,°C$ T_b rose to above $40\,°C$. The thermal conductance was not constant below the lower critical temperature. At $T_a = 5-10\,°C$ it was 16% below the expected value. Total evaporative water losses (TEWL) did not differ significantly at ambient temperatures from $5-28\,°C$ (mean value 0,779 ml H_2O per kg and hour). Higher ambient temperatures caused a steep increase in TEWL (to the 4,6fold at $38\,°C$). However, at $T_a = 38\,°C$ only $2/3$ of the endogenous heat production could be dissipated by evaporation. TEWL at high ambient temperatures was mainly raised by an increase of the respiratory frequency; also salivation occurred. Mean resting heart rate within the TNZ was $110,9$ beats $\cdot min^{-1}$; minimal values were measured with $80-85$ beats $\cdot min^{-1}$. Between $T_a = 25-20\,°C$ the increased oxygen transport was achieved by a rise of the oxygen pulse, whereas from $20-15\,°C$ cardioacceleration was the most important factor. The results are discussed with special regard to the ecological situation in the tropical rainforest and the different modes of locomotion within the prosimian families Galagidae and Lorisidae.

Introduction

Present data suggest different levels of basal energy metabolism within the prosimian families Lorisidae and Galagidae: Whereas the slow-moving Lorisidae have a basal heat production of only $40-60\%$ of the mammalian standard (Hildwein and Goffart 1975; Müller 1975, 1979; Whittow et al. 1977), the active leaping Galagidae show a reduction to $70-80\%$ of the standard (Hildwein 1972; Dobler 1976, 1978). Additionally in the Galagidae the body temperature is at a higher level and is regulated more precisely (Dobler 1978). These physiological differences are presumably connected with the essential differences in the mode of locomotion within the two families (Müller 1979).

The hitherto existing studies, however, only dealt with the smaller species of bushbabies, thus leaving the possibility that the different levels occurred at least partly due to the different body masses of the investigated species. To fill this gap we, therefore, examined the basal metabolism and the thermoregulatory abilities of the thick-tailed bushbaby; this species is of similar size as potto and slow loris and is midway between the two types of locomotion (Bearder and Doyle 1974).

Materials and methods

Three adult male *G. crassicaudatus* were used in this study. The animals were caught in Kenia during spring 1978. From June 1978 on they were kept single in cages of $150 \times 100 \times 60$ cm in our laboratory in Tübingen. The room temperature was regulated at $25 \pm 1\,°C$ and the relative humidity at $70 \pm 10\%$. The light regime followed a 13:11 L:D cycle with the dark phase from 7 p.m. till 6 a.m. Food consisted mainly of bananas, apples, carrots, lettuce and mealworms; it was supplemented with minced meat and a pap of baby food, honey and raw eggs. Drinking water was always available. Vitamins and minerals were regularly added. Under these conditions the animals kept a constant mean body mass of 950 g.

For measuring the rectal temperatures we used a thermistor (Testotherm; digital 2500) which could be inserted to a depth of 8 cm. To reveal the daily variations, the body temperatures were taken in the animal room; at most 4 measurements were made during a 24 h period. Body temperatures after exposure to the various ambient temperatures were measured within 1 minute after opening the temperature cabinet.

For the simultaneous registration of oxygen consumption, heart rate and evaporative water loss the bushbabies were placed in a plexiglass container (volume 21,5 l) within a temperature cabinet (Ehret), where ambient temperatures could be regulated to $\pm 0,5\,°C$; the temperature within the animal box was continuously monitored.

Dried air ($CaCl_2$-column) was drawn through the animal box at constant rates from $80-187$ l/h (STPD) depending on the various temperatures; flow rates were controlled with Rotameters (Rota). O_2-consumption was measured with a Beckman G 2 oxygen analyzer. All values of O_2-uptake were converted to STPD, but no correction was made for the small error introduced if the respiratory quotient did not equal 1.

Evaporative water losses were calculated from the different water content of the air entering and leaving the animal container. For this purpose two measuring units, each consisting of a hygro- and temperature-sensor (Nova-Sina equi-Hygro-Scope, eMPF-4/TAL), were placed in the air stream. The measured data were continuously monitored with a multi-channel recorder (Fig. 1). By knowing the rate of air flow, the relative humidities and the temperatures of the incoming and outgoing air it was possible to calculate the amount of water evaporated by the animals. Urine and faeces were caught under paraffin oil, such minimizing their contribution to the water vapour pressure. Relative humidity in the animal box thus varied from $38-98\%$ depending on the various temperatures and could be kept below the dew point by adjusting the air flow.

The heart rate was measured by telemetry in the manner described elsewhere (MÜLLER et al. 1979).

All experiments were performed during the resting period of the bushbabies (8 a.m. -3 p.m.). At ambient temperatures below $35\,°C$ the animals usually fell asleep after about 30 minutes. Evaluation of oxygen consumption, heart rate and evaporative water loss, however, only started after an equilibration time of 2 hours. If not stated otherwise, the given data represent mean values during the subsequent period of about 3 hours, except for high ambient temperatures, where some experiments had to be stopped prematurely to spare the animals.
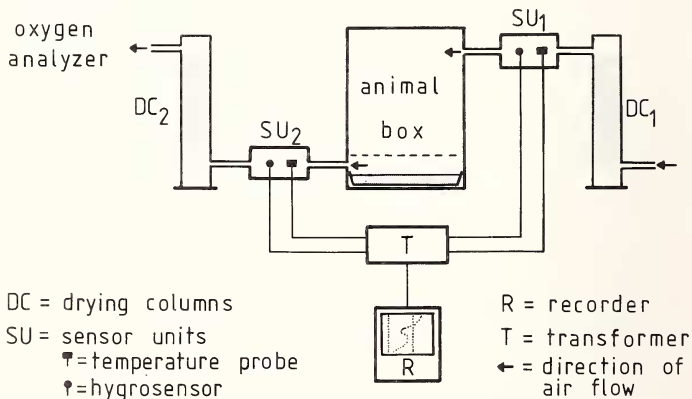

Fig. 1. Experimental arrangement for the continuous measurement of evaporative water loss. The bushbabies lay on a wire mesh which was coated with synthetic resin. Faeces and urine were caught under paraffin oil

Results

Daily cycle of body temperature

The body temperature of the thick-tailed bushbaby follows a marked day-night-rhythm (Fig. 2). The mean T_b during the resting period was $36,6 \pm 0,5\,°C$; the lowest values were found between 7–8 a. m. with $35,6\,°C$. During the activity at night the mean T_b rose to $37,7 \pm 0,3\,°C$; the highest body temperatures were measured at 11 p. m. and 4 a. m. with $38,3\,°C$. However, if the animals were excited, the body temperature sometimes exceeded $39\,°C$.
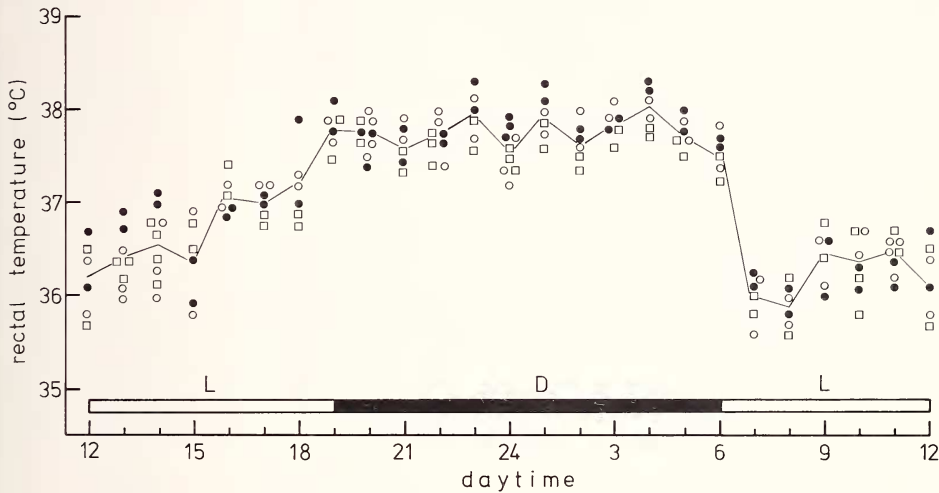

Fig. 2. Daily cycle of rectal temperature of three male *G. crassicaudatus*. Single measurements (symbols) and mean values (line). □ = male 1 (920 g); ○ = male 2 (900 g); ● = male 3 (1020 g)

Thermoregulation

Exposure to ambient temperatures from $5-28\,°C$ did not affect the body temperature; it remained within the normal resting range (Fig. 3). Ambient temperatures above $28\,°C$, however, led to a marked increase of T_b. At $T_a = 35\,°C$ the bushbabies showed signs of severe heat stress and increasing restlessness. After $3\,^1/_2$ h at $T_a = 38\,°C$ the body temperature of one animal had risen to $41,4\,°C$; the muscles were nearly atonic and – back in its cage – the bushbaby immediately began to drink.

Oxygen consumption

Oxygen consumption was lowest at ambient temperatures from $25-31\,°C$ (Fig. 4). Within this thermoneutral zone the mean O_2-uptake was $0,434$ ml $O_2 \cdot g^{-1} \cdot h^{-1}$ (= $8,72$ kJ $\cdot kg^{-1} \cdot h^{-1}$); this is only 71% of the value predicted from body mass (KLEIBER 1961). Below the lower critical temperature ($25\,°C$) O_2-consumption followed the regression line (method of least squares): Y (ml O_2 per g and h) = $0,941 - 0,019 \cdot T_a$ ($°C$), correlation coefficient = $-0,99$.

Between $T_a = 31-35\,°C$ O_2-consumption rose continuously and at $T_a = 38\,°C$ the increased internal heat production led to the above mentioned threatening rise of the body temperature.
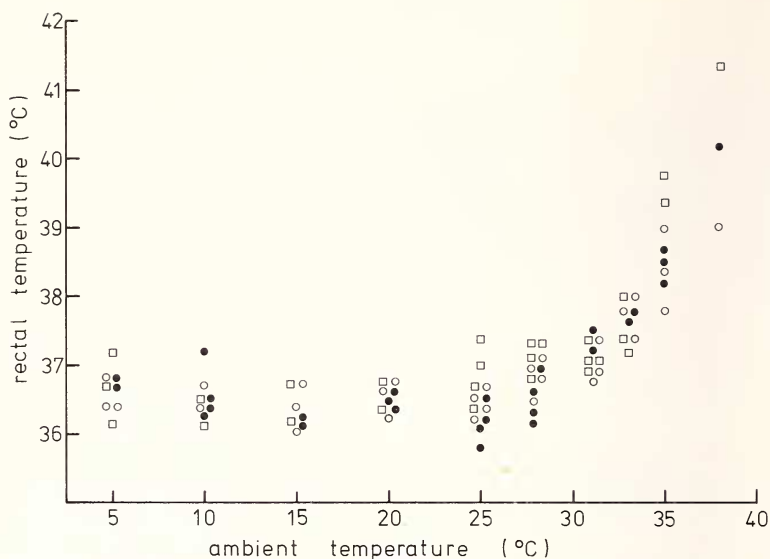
Fig. 3. Rectal temperatures after exposure (3–6 h) to ambient temperatures from 5–38 °C. Same symbols as in Fig. 2
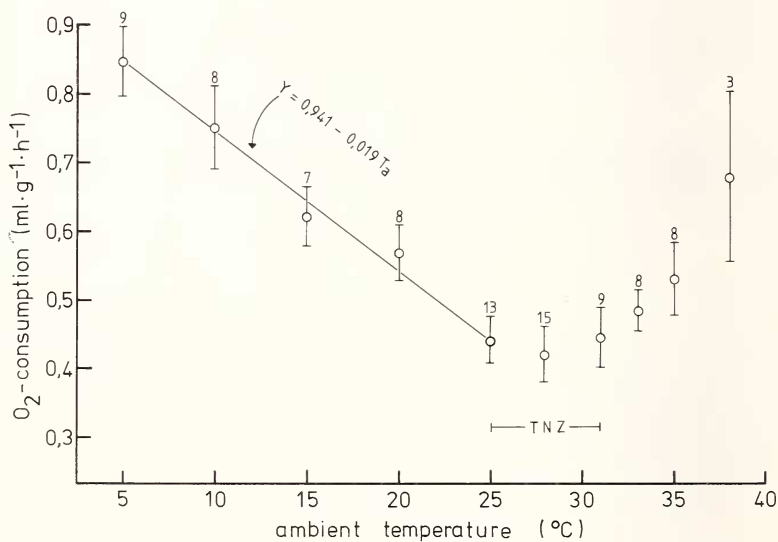

Fig. 4. Oxygen consumption (mean ± S. D.) at ambient temperatures from 5–38 °C. The small figures indicate the number of measurements at the various ambient temperatures. Also given is the range of the thermoneutral zone (TNZ) and the regression line for temperatures below 25 °C

Thermal conductance

The thermal conductance was not constant below the lower critical temperature (Table 1). After a marked initial drop at ambient temperatures from 25–20 °C, the decrease became less between 20–10 °C. A further fall of T_a from 10–5 °C did not affect the conductance.

Table 1

Thermal conductance (C=$\dfrac{V_{O_2}}{T_{re}-T_a}$ ml $O_2 \cdot g^{-1} \cdot h^{-1} \cdot °C^{-1}$) below the thermoneutral zone

Mean values ± S.D.

T_a(°C)	5	10	15	20	25
C	0,027 ± 0,002 n = 8	0,027 ± 0,002 n = 8	0,03 ± 0,003 n = 7	0,033 ± 0,003 n = 8	0,039 ± 0,004 n = 12
C/C_{th}*	0,84	0,84	0,94	1,03	1,22

*C_{th} = 1,02 · $W^{-0,505}$ (Herreid and Kessel 1967).

The variable nature of the thermal conductance in G. *crassicaudatus* leads to the situation that at T_a = 25 °C it is 22 % above and at T_a = 5–10 °C 16 % below the expected value according to the formula of HERREID and KESSEL (1967).

Evaporative water loss

The amount of water lost by evaporation was not significantly different at ambient temperatures from 5–28 °C (Table 2). Within this temperature range the average evaporative water loss was 0,779 ml $H_2O \cdot kg^{-1} \cdot h^{-1}$. At higher ambient temperatures TEWL increased steeply to about the 2,5fold at T_a = 35 °C and to the 4,6fold at T_a = 38 °C. However, as can be seen from the ratio E/M, at T_a = 33 °C only ¹/₃ and at T_a = 38 °C ²/₃ of the internal heat production could be dissipated through evaporative pathways.

Table 2

Evaporative water loss (TEWL) and ratio of heat loss via evaporation to internal heat production (E/M)

Mean values ± S.D.

T_a (°C)	n	TEWL $\dfrac{ml\ H_2O}{kg \cdot h}$	$\dfrac{mg\ H_2O}{ml\ O_2}$	E/M
5	8	0,79 ± 0,13	4 ± 0,53	0,11
10	7	0,82 ± 0,12	4,47 ± 0,83	0,13
15	7	0,71 ± 0,09	4,9 ± 0,89	0,14
20	8	0,79 ± 0,14	5,83 ± 1,12	0,17
25	12	0,77 ± 0,08	7,1 ± 0,69	0,21
28	13	0,79 ± 0,09	7,93 ± 0,75	0,22
31	9	1 ± 0,18	10,33 ± 1,67	0,27
33	8	1,3 ± 0,12	11,17 ± 0,46	0,32
35	8	1,94 ± 0,34	14,63 ± 1,17	0,44
38	3	3,61 ± 0,96	21,63 ± 0,67	0,63

Thermoregulatory behaviour

At ambient temperatures from 15–28 °C the bushbabies slept in a curled up position on the side, the long bushy tail covering parts of the body and the face. When exposed to lower temperatures the animals several times were seen sitting on the back but still showing the curled up posture. Shivering then was clearly visible.

At temperatures above 28 °C the bushbabies gradually gave up the ball-like posture to

facilitate heat loss. At $T_a = 35\,°C$ they started salivating and licking hands and belly; they were repeatedly watched rubbing the wetted hands over the face. Additionally the respiratory frequency was raised: At $T_a = 38\,°C$ periods of panting occurred with more than 250 breaths $\cdot$ min^{-1} (visual observation).

Heart rate

Within the thermoneutral zone the average heart rate was $110,9 \pm 16,2$ beats $\cdot$ min^{-1} (Fig. 5). Minimal values, however, were considerably lower: $80-85$ beats $\cdot$ min^{-1} for periods of at least 5 minutes. With falling ambient temperatures the mean heart rate rose to about 160
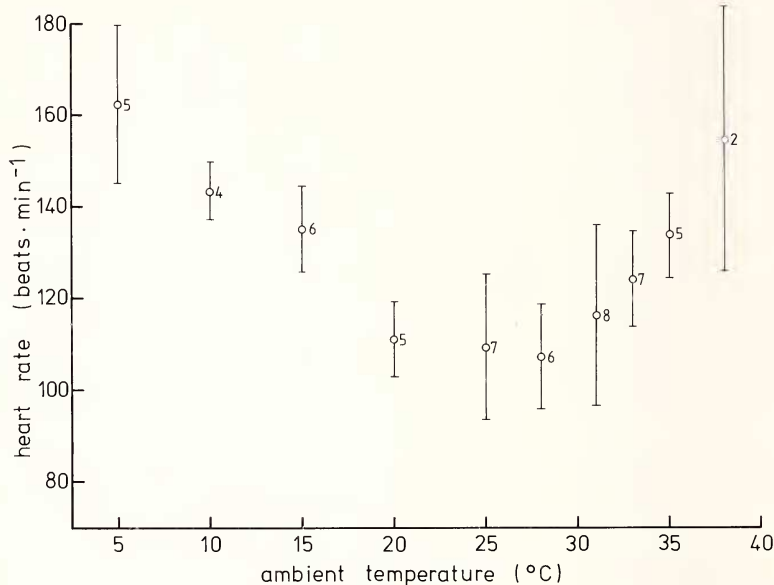

Fig. 5. Heart rate (mean $\pm$ S. D.) at ambient temperatures from $5-38\,°C$. The small figures indicate the number of measurements at the various ambient temperatures. From each experiment the mean value was calculated over a period of at least 40 min
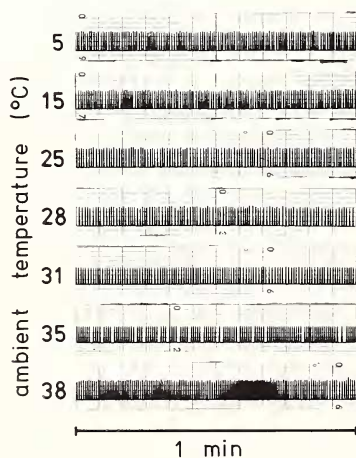

Fig. 6. Heart beat pattern at various ambient temperatures. Note the marked respiratory arrhythmia which became attenuated only at low and high ambient temperatures

beats · min^{-1} at T_a = 5°C, the increase between 25–20°C, however, being only slight. High ambient temperatures caused a sharp rise of the heart rate which occasionally exceeded 300 beats · min^{-1}. Over the whole range of ambient temperatures the heart beat pattern showed respiratory arrhythmia indicating a predominance of the vagus nerve (Fig. 6).

Oxygen transport in the blood

From 25–31°C the mean oxygen pulse was 62,2 μl · beat^{-1}, differing not much from the value predicted from body mass if calculated after the combined formulas of KLEIBER (1961) and WANG and HUDSON (1971). Between 25–20°C the oxygen pulse rose markedly, whereas the contribution of heart rate to the increased oxygen transport was only 0,7% (Table 3). When the ambient temperature dropped from 20–15°C, however, the oxygen pulse decreased and accordingly the increase of the heart rate became the most important factor for the enlarged oxygen transport. To a further fall of the ambient temperature the bushbabies reacted with both cardioacceleration and a rise of the oxygen pulse.

Table 3

Oxygen pulse and contribution of heart rate to the increased oxygen transport below
the thermo neutral zone

Calculated after the formula of BARTHOLOMEW and TUCKER 1963

T_a	mean heart rate	oxygen pulse	contribution of heart rate (%)	
(°C)	beats · min^{-1}	μl · beat^{-1}	A*	B*
5	162,3	83,4	57,6	70,3
10	143,3	79	52	41,1
15	135,1	72,6	56,6	147,2
20	111,1	78	0,7	0,7
TNZ	110,9	62,2	–	–

* A = in relation to the TNZ; B = in relation to the next higher T.

Discussion

From this study it emerges that the basal metabolic rate of the thick-tailed bushbaby is reduced to about the same level below the value predicted from body mass as it is in the other Galagidae (20–30%); it thus differs markedly from similar-sized Lorisidae, where the reduction amounts to 40–60%. It, therefore, can be excluded that the different levels of BMR in these two prosimian families are based upon the different sizes of the various species. It seems rather probable that the differences are related to the different types of locomotion as was already suggested by MÜLLER (1979): The Galagidae try to escape from predators mainly by quick flight using their ability for jumping over long distances; the Lorisidae, on the other hand, try to avoid detection by enemies, a strategy which is largely favoured by their sluggish movements (CHARLES-DOMINIQUE 1971).

The higher degree of alertness and mobility in the Galagidae might only be compatible with a higher level and a more precise regulation of the body temperature, a situation which also requires a higher basal heat production. This view is supported by our results in *G. crassicaudatus*: Like in other Galagidae the resting as well as the activity level of the body temperature is about 1–2°C above that of the Lorisidae (HILDWEIN and GOFFART 1975; WHITTOW et al. 1977; DOBLER 1978; MÜLLER 1979; this study). The nycthemeral variation of the

body temperature in G. crassicaudatus coincides with the "Alternans"-type of activity found in this species (WELKER 1977).

Whereas in the Lorisidae long time exposure to low ambient temperatures usually leads to a considerable cooling of the body shell (HILDWEIN and GOFFART 1975; MÜLLER 1979), the thick-tailed bushbaby – like its smaller relatives – regulates its body temperature at the normal resting level. The finding, however, that at mildly cold temperatures the thermal conductance of G. crassicaudatus decreases, suggests a cooling of at least parts of the body shell. A decreasing conductance at falling ambient temperatures has also been found in the slow loris (MÜLLER 1979) and the Coati (CHEVILLARD-HUGOT et al. 1980). Anatomical structures in the limbs (rete mirabile) which could serve as counter current heat-exchangers as was described for the slow loris (MÜLLER 1979) apparently are missing in the Galagidae (WISLOCKI and STRAUS 1932).

The thick woolly fur of G. crassicaudatus provides an excellent protection against heat losses. Exposure to $T_a = 5\,°C$ only leads to a 2fold increase in heat production if compared to the basal level within the thermoneutral zone. In the greater bushbaby this zone of minimal O_2-uptake extends from $25-31\,°C$; as already mentioned above the BMR is about 30 % below the value predicted from body mass. In the smaller species of bushbabies DOBLER (1978) found thermoneutral zones from $28-34\,°C$ (G. s. senegalensis), $28-35\,°C$ (G. s. moholi) and $30-35\,°C$ (G. demidovii). The lower range of the TNZ in G. crassicaudatus is probably a consequence of its bigger size and the high insulative value of its fur. In addition the ability of the thick-tailed bushbaby to dissipate excessive heat by evaporation is limited: At $T_a = 33\,°C$ only $1/3$ and at $T_a = 38\,°C$ only $2/3$ of the endogenous heat production can be dissipated by evaporation. These values essentially agree with the results in other Galagidae (DOBLER 1978) and in the Lorisidae (HILDWEIN and GOFFART 1975; MÜLLER 1979). They are also in accordance with the findings of HILEY (1976) that the sweat glands of G. crassicaudatus even after local irridation with infrared light did not show effective sweating. MÜLLER (1979) already pointed to the fact that the prosimians mainly rely on panting as means of heat dissipation, whereas the higher primates as a rule increase evaporative cooling by sweating.

It seems that many prosimians – mainly due to the nocturnal activity – during their evolution were not forced to develop highly effective ways for evaporative cooling. The dense fur of most species rather suggests heat conservation as their main problem. With regard to these questions it would be very desirable to have more information about the basal energetics and the thermoregulatory capacities of malagasy lemurs, especially about the day-active species. One might speculate that in the very complex ecosystem of the tropical rainforest (where most prosimians live) a strong selective pressure forces to a most economical exploitation of the energy resources. The most energy consuming task for homeothermic mammals, however, surely is to strictly maintain the body temperature at a high level. The rather stable climatic conditions in the tropical rainforest, therefore, could have favoured a tendency towards lower body temperatures and a somewhat "careless" thermoregulation; this would allow to reduce the basal heat production, thus saving considerable amounts of energy (MÜLLER and KULZER 1977). The reduced heat production again could be compensated by a good thermal insulation. This would explain the otherwise strange finding that many mammals – though living in the tropical rainforest – have a dense woolly fur. In these circumstances the variable nature of the thermal conductance in G. crassicaudatus (and other mammals) is a very effective means to deal with both aspects of thermoregulation, i. e. improving heat conservation at low ambient temperatures and increasing heat dissipation in a warm environment. These considerations might also hold true for mammals with specialised food habits as was discussed by McNAB (1978).

The mean resting heart rate of the thick-tailed bushbaby within the thermoneutral zone is about 25 % below the mass-specific value (as calculated after WANG and HUDSON 1971); minimal values are even considerably lower. This is surely related to the reduced basal metabolism and agrees with findings in the Springhare (MÜLLER et al. 1979), the Coati